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REFLEXES INVOLVING THE EXTERNAL URETHRAL SPHINCTER IN THE CAT

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Barrington (1915, 1921, 1928, 1931, 1941) ultimately came to the belief that seven reflexes are involved in the act of micturition in the cat. These micturition reflexes are tabulated in Table 1. Barrington's conception was based on studies of the pressure and volume of fluid in the urinary bladder and of the resistance to the flow of fluid through the urethra.

TABLE 1. Micturition reflexes in the cat according to Barrington (the terminology is that of Barrington)

Reflex	The stimulus	Ingoing path	'Centre'	Outgoing path	Response of the effector
1	Distension of the bladder	Pelvic nerves	Hind-brain	Pelvic nerves	Contraction of the bladder
2	Running water through the urethra	Pudendal nerves	Hind-brain	Pelvic nerves	Contraction of the bladder
3	Distension of the proximal urethra	Hypogastric nerves	Lumbar cord	Hypogastric nerves	Slight transitory contraction of the bladder
4	Running water through the urethra	Pudendal nerves	Sacral cord	Pudendal nerves	Relaxation of the urethra
5	Distension of the bladder	Pelvic nerves	Sacral cord	Pudendal nerves	Relaxation of the urethra
6	Distension of the bladder	Pelvic nerves	Sacral cord	Pelvic nerves	Relaxation of the plain muscle of the urethra in its proximal third
7	Running water through the urethra	Pelvic nerves	Sacral cord	Pelvic nerves	Contraction of the bladder

He was unable to observe directly the behaviour either of the striped muscle of the external urethral sphincter or of the smooth muscle of the urethral wall which is thought to act as an internal urethral sphincter. As a consequence he was not able to separate with certainty the functional roles of these two sphincters. Now, however, the method of electromyography can be used to study directly the activity of the external urethral sphincter. Moreover, the timing of the responses of this muscle can be accurately determined. This we have done in decerebrate cats. Our results call for some modification of Barrington's scheme of reflexes. Some clarification also emerges about the nature of the adequate stimuli for certain of the reflexes.

The external urethral sphincter in the cat consists of striped-muscle fibres encircling the urethra in the substance of the urethral wall. Diagrams of the anatomical relations and of the innervation of the parts in both sexes are given by Evans (1936) and by Langworthy, Kolb & Lewis (1940). The external sphincter does not lie against the neck of the bladder but distally, with about 1½ cm of 'proximal urethra' between it and the bladder.

METHODS

Decerebrate cats of both sexes were used. The urethra was exposed throughout its length by a mid-line ventral incision, the two halves of the symphysis pubis were separated, and the retropubic fat was removed by blunt dissection.

Spinal anaesthesia, and section of the lumbar sympathetic outflow and of the pelvic nerves, were carried out, when called for, by methods previously described (Garry, 1933). Spinal transection was carried out under full ether anaesthesia by extradural ligature of the cord after opening the vertebral canal.

A twin-bore cannula was inserted into the bladder through a cut in the proximal urethra, and was tied in so that no fluid could pass from bladder to urethra. One channel of the cannula was connected to a reservoir of Ringer's fluid; by raising and lowering this reservoir (range 0–40 cm) the bladder could be filled and emptied. Movement of the reservoir operated a potentiometer through a system of pulleys. The height of the reservoir, the bladder-filling pressure, was then displayed on an oscillograph. A float volume-recorder, connected to the reservoir, measured changes in bladder volume and gave an electrical signal by means of a side arm which moved in a trough containing glycerine, which acted as a fluid potentiometer. The other channel of the cannula was connected by a rigid polythene tube of minimum distensibility to an electronic transducer-manometer which gave a continuous record of the pressure within the bladder.

Perfusion of the lumen of the urethra was carried out through a single-bore cannula tied into the proximal end of the distal urethra, with its opening pointing away from the bladder. This cannula was connected through a 3-way tap to a reservoir of Ringer's fluid which could be raised from 0 to 60 cm. The pressure applied to the urethra could be increased gradually by raising the reservoir, or suddenly by first raising the reservoir and then turning a tap. The volume of fluid flowing along the urethra was recorded by a float volume-recorder connected to the reservoir.

The recording electrodes were made from stainless steel pins, insulated to the tips, and independently mounted on fine springs. Two electrodes were used, their points resting lightly on the surface of the exposed external sphincter at positions found by trial to give a suitable record. The muscle was kept covered with a layer of warm liquid paraffin.

The records were made on a 4-channel ink-writing pen oscillograph.

RESULTS

Reflexes from bladder to the external urethral sphincter

The external urethral sphincter, like the external anal sphincter (Bishop, Garry, Roberts & Todd, 1956), shows a resting tonic discharge. This discharge is of low frequency when the bladder is empty. As the bladder begins to fill there is an increase in the frequency of the discharge from the sphincter. The intravesical pressure, after a slight initial rise, remains constant as filling continues. After a time two marked responses take place, though both take several seconds to develop fully. (1) Sphincter activity first decreases somewhat and then ceases entirely (Barrington's fifth reflex), and (2) the bladder pressure rises sharply, leading to the return of fluid from the bladder to the reservoir (Barrington's first reflex). Sphincter activity remains in abeyance throughout the phase of raised bladder pressure (Fig. 1).

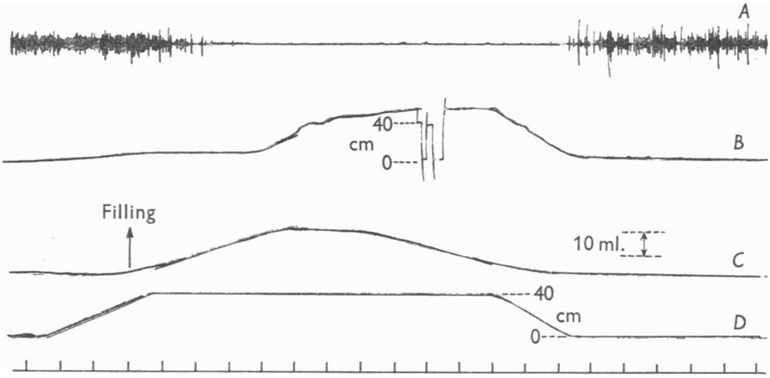

Fig. 1. Decerebrate male cat: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure with calibration in cm H_2O; *C*, change in bladder volume; *D*, height of reservoir. Contraction of bladder is isotonic and reduction in sphincter activity precedes rise in bladder pressure by approximately 25 sec. In all figures, time marker = 10 sec.

Usually the response of the sphincter and the response of the bladder appear to start at about the same time: but often, as in Fig. 1, the reduction in sphincter activity clearly precedes the rise in bladder pressure and complete inhibition may occur while the volume of the bladder is increasing and the intravesical pressure is still constant. When the evacuation of the partially filled bladder is prevented by obstruction of the urethra, the detrusor muscle exhibits a series of spontaneous isometric contractions (Mellanby & Pratt, 1940). In these circumstances the isometric contractions are also accompanied by reduced sphincter activity, which, in this case, develops during a period of constant bladder volume and rising intravesical pressure (Fig. 2).

Spinal transection at the lower thoracic level abolishes the reflex contraction of the bladder in response to filling, at least for the duration of an acute experiment: Barrington (1921) found that this reflex was still in abeyance 35 days after section of the cord. However, filling the bladder still causes a reduction in the activity of the external sphincter. The reduction in the tonic activity of the external sphincter is not so marked as it is in cases where contraction of the bladder takes place (Fig. 3).

General anaesthesia with ether was used before cutting the spinal cord. The administration of ether itself abolished the tonic activity of the sphincter, but on disconnecting the supply of ether the tone returned quickly to the sphincter and it was fully present well within 2 hr of the transection.

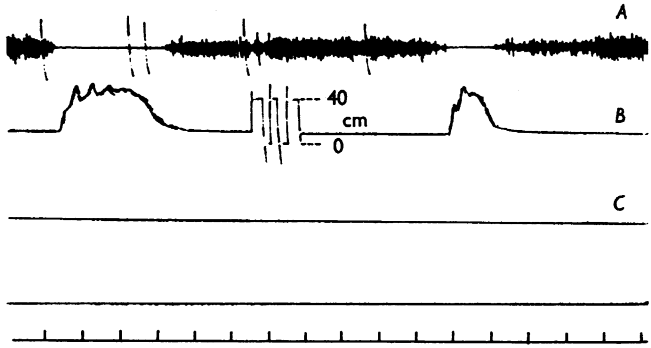

Fig. 2. Decerebrate male cat: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure with calibration in cm H_2O; *C*, change in bladder volume—contraction is isometric since outflow from the bladder is prevented. Reduction in sphincter activity occurs without any change in the volume of the bladder.

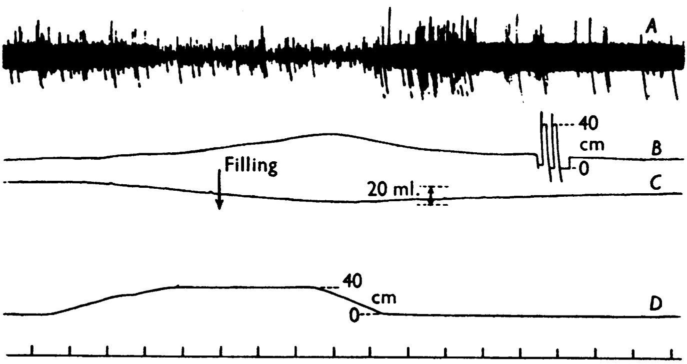

Fig. 3. Decerebrate male cat, spinal cord cut at lower thoracic level: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure with calibration in cm H_2O; *C*, change in bladder volume; *D*, height of reservoir. Reflex contraction of bladder absent; reduction of sphincter activity accompanies distension of bladder.

Reflexes from the urethra

If, when the bladder is empty or contains only a small volume of fluid, an attempt is made to force fluid along the distal urethra with gradually increasing pressure, there is then a progressive *increase* in the activity of the external sphincter muscle (Fig. 4). The sphincter guards against the escape of fluid. This increased activity in the sphincter occurs both when fluid actually flows along the urethra, and also when the urethra is tied distal to the external sphincter so that no fluid passes and the urethra is only distended. If the urethra is not tied, the increase in sphincter activity occurs before the fluid begins to flow. A major component of the adequate stimulus for the reflex increase in sphincter activity must therefore be the stretching of the structures in the wall of the urethra.

Our findings are consistent with those of Evans (1936). He recorded the electrical activity in the nerves supplying the bladder and urethra in cats, and reported that sudden distension of the bladder reduced the tonic outgoing discharge along the pudendal nerves, whereas attempts to force fluid along the urethra with a syringe always increased this discharge.

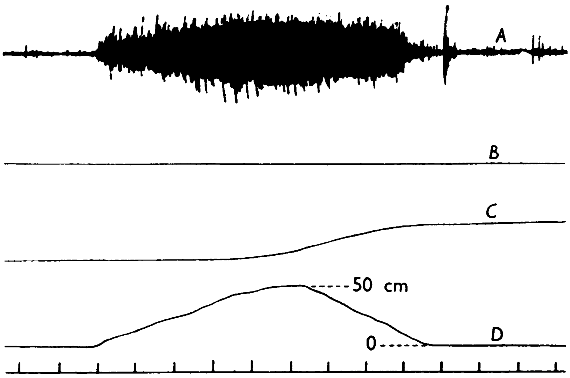

Fig. 4. Decerebrate female cat, bladder empty: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure; *C*, volume of fluid which has passed through the urethra—the change in level indicates flow; *D*, height of reservoir connected to urethra. Increasing pressure applied to the distal urethra induces activity in the external sphincter corresponding to the increase in pressure: flow along the urethra starts when the pressure reaches 50 cm H_2O and continues even while the pressure is reduced, although the external sphincter is still active.

Pressures in excess of 40–50 cm H_2O can force fluid along the urethra past the powerfully contracted external sphincter. If the applied pressure is now reduced, fluid continues to pass along the urethra at pressures which are less than those needed to start the flow. This behaviour is no indication of a true inhibition of the activity in the external sphincter. The external sphincter is still active. The slight diminution in activity of the sphincter which occurs sometimes after the flow has started may be attributed to the reduction in the distending pressure within the urethra which is a consequence of the flow. In our experiments the signal indicates the height of the reservoir. The distending pressure applied to the urethra will be less than that indicated by the signal by an amount dependent on the rate of flow and on the resistance of the connecting tubing.

On the other hand, flow of fluid along the urethra and distension of the urethra fail to elicit activity in the external sphincter if the tone in this muscle is already absent or reduced in reflex response to an increase in the tension in the bladder wall arising either from contraction or from distension of the bladder (Fig. 5). In other words, when Barrington's fifth reflex—dilatation of the urethra in response to distension of the bladder—is in action, forcing fluid along the urethra cannot cause contraction of the external urethral sphincter.

When there is a considerable volume of fluid in the bladder, running fluid through the urethra evokes a sustained contraction of the bladder—

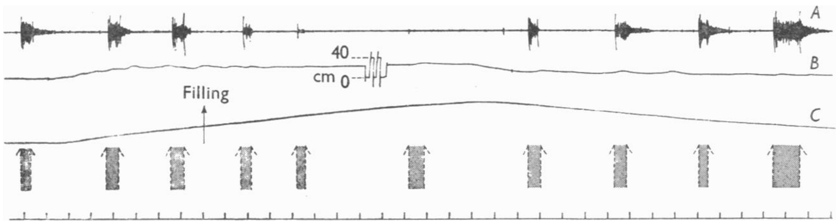

Fig. 5. Decerebrate female cat: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure (cm H_2O); *C*, change in bladder volume. The urethra was tied distally: at the times, and for the durations indicated, the pressure in the distal urethra was raised abruptly to 60 cm H_2O. The response of the external sphincter to distension of the urethra dies out as the bladder fills and reappears as the bladder empties.

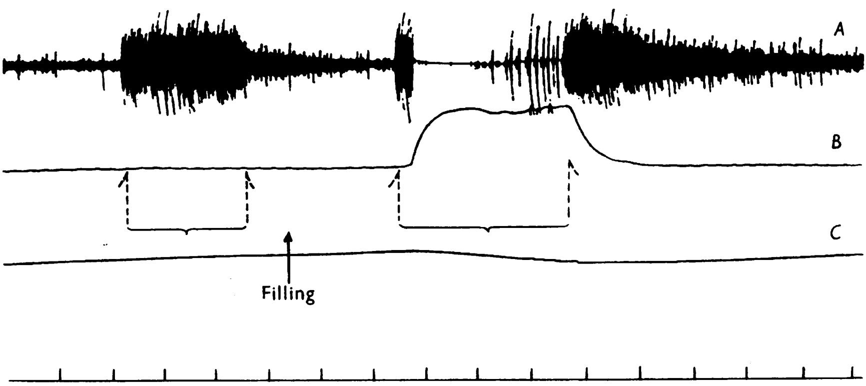

Fig. 6. Decerebrate male cat: *A*, action potentials from external urethral sphincter; *B*, intravesical pressure; *C*, change in bladder volume. Fluid is running into the bladder; at the times, and for the durations shown by the vertical dotted lines, the distal urethra is suddenly distended by a pressure of 40 cm H_2O. In the first instance there is no contraction of the bladder and the activity of the sphincter is greatly augmented. In the second instance, when the bladder is somewhat fuller, distension of the urethra initially augments the activity of the external sphincter but, when the bladder responds by contraction, the activity of the external sphincter ceases until the bladder has emptied.

Barrington's second and seventh reflexes. This reflex contraction of the detrusor muscle of the bladder, in response to the passage of fluid distally along the urethra, develops, however, more slowly than the 'guarding' burst of activity in the external sphincter. Under such circumstances, then, there is at first an increase in sphincter activity and this later disappears completely as the bladder starts to contract. When the bladder relaxes once more, activity of the sphincter reappears (Fig. 6).

If the reflex effect of tension in the wall of the bladder is eliminated, e.g. by emptying the bladder, by removing the bladder or by cutting the pelvic nerves, the only response to flow of fluid along the urethra is increased activity in the external sphincter. In a cat recently dead a much lower pressure is needed to force fluid distally along the urethra than in a decerebrate cat. As in the living animal, however, a greater pressure is required to start the flow than to maintain it.

DISCUSSION

The lower urinary tract has two main functions, the maintenance of urinary continence, and the periodic emptying of the bladder. These two functions require close co-ordination between the activity of the bladder wall and the behaviour of the sphincters which govern the urethra. Barrington analysed the co-ordination which operates during micturition. The present results support his findings in general but they suggest the need for some amplification and modification of his basic scheme, and for more consideration of the factors concerned not only with micturition but also with urinary continence.

Under normal conditions for most of the time the smooth muscle of the bladder wall does no more than exert a slight degree of pressure on the contents. Urinary continence is achieved by this absence of active contraction and by the closure of the sphincters of the urethra. Electromyography shows that the external urethral sphincter has a continuous tone which is of low degree when the bladder is empty. This tone increases somewhat in the early stages of bladder filling. At this stage any attempt to force fluid distally along the urethra provides an effective stimulus to increase the activity of the external sphincter. This behaviour of the external sphincter will operate to maintain urinary continence when, in the intact animal, the bladder is filling from the ureters. The external urethral sphincter in the cat is able to withstand a perfusion pressure of about 50 cm H_2O; if the pressure becomes greater, urine escapes in drops as in overflow incontinence. Presumably, however, reflex micturition normally occurs long before intravesical pressures of this magnitude are reached.

The initial stimulus to reflex micturition seems to be the attainment of a critical degree of bladder filling. The detrusor muscle then responds by rhythmical waves of contraction or by a sustained contraction, and the sphincter responds by relaxation. Relaxation of the external urethral sphincter may be brought about either by the introduction of an adequate volume of fluid into the bladder, without any rise in intravesical pressure, or by a rise in intravesical pressure without alteration in volume. The receptors for this reflex must therefore respond both when the contractile elements in the bladder wall are actively contracting and also when the bladder wall is being passively stretched as in the acute spinal cat. Tension receptors in series with the contractile elements of the bladder wall would be expected to react in both these two sets of circumstances (Garry, Roberts & Todd, 1957). Iggo (1955) has evidence, based on recordings from sensory nerves, for the existence of such receptors both in the bladder wall and in the stomach wall. Nathan (1956) observed that the desire to micturate was evoked in man when the wall of the bladder was stretched and also when the bladder contracted.

The main point at issue between our findings and those of Barrington concerns the existence of his fourth micturition reflex. Barrington thought that, independently of any other factor, the flow of urine along the distal urethra reflexly brought about relaxation of the external urethral sphincter, both paths being in the pudendal nerves. We, on the other hand, were not able at any time to show inhibition of activity in the external sphincter in response to perfusion of the urethra, apart from the inhibition which was associated with a rise of tension in the wall of the bladder. In other words, passage of fluid into the urethra had first to cause contraction of the bladder by Barrington's second reflex; then the increased tension in the bladder wall brought about relaxation of the external sphincter by his fifth reflex. Indeed, Barrington (1928) noted that, when the urinary bladder could no longer contract, owing to division of the pelvic nerves or to section of the spinal cord, then it was more difficult to elicit his fourth reflex. He even suggested that, normally, contraction of the bladder reinforces the fourth reflex; in his own terminology, the fifth reflex reinforces the fourth. The main evidence which Barrington put forward for the existence of an independent fourth reflex, with both paths in the pudendal nerves, was that when gradually increasing pressure of fluid was applied to the distal urethra a greater pressure was needed to start the flow than was required to maintain it when once started. In fact, however, a difference between the pressure needed to start the flow and the pressure necessary to maintain it has been shown to exist both in conditions of high, sustained activity of the external sphincter and in conditions of total absence of any striped-muscle activity at all, in the recently dead cat.

Langworthy, Drew & Vest (1940) perfused the urethra of decerebrate cats. As the pressure was raised the perineal muscles contracted spasmodically and the fluid escaped in spurts. This was followed by a steady flow. When the pressure was lowered the flow continued at a pressure less than that required to start the flow. They found also that sudden increases of pressure in the urethra evoked spasm of the perineal muscles; such responses could not be elicited when the bladder was full. Barrington fully appreciated that the evidence for the existence of his fourth reflex was indirect, but he had no way of telling that this evidence was not valid. Denny-Brown & Robertson (1933) state categorically that the presence of fluid in the posterior urethra of spinal man cannot cause relaxation of the external urethra sphincter: only contraction of the detrusor muscle relaxes the external sphincter.

The fact that a flow of fluid along the urethra can be maintained by driving pressures which are less than the pressure necessary to initiate flow can be shown to be a consequence of the general physical properties of tubes with circular muscle in their walls (Roberts, unpublished). The curve for the combined tension/length relationship for the muscular and elastic components of the wall will have a shoulder or hump on it, with a point of inflexion. Consequently the critical opening pressure will differ from the critical closing pressure and there will be a range of pressures in between at which flow can continue, provided it has first been initiated by raising the driving pressure above the critical opening pressure. It is not necessary to postulate a reflex mechanism, such as Barrington's fourth reflex, whereby flow of fluid along the urethra might lead to reflex inhibition of activity of the sphincter. The fact that the activity does, in fact, sometimes diminish somewhat in these conditions may be taken as a consequence of the reduced sensory drive corresponding to the reduction in distending pressure. It is not necessarily a result of an inhibitory effect of impulses from receptors sensitive to the flow of fluid along the urethra, even if such receptors can be shown to be present.

Barrington, in his preoccupation with reflexes promoting emptying of the bladder, perhaps gave too little consideration to guarding reflexes which *prevent* emptying of the bladder. Were his fourth reflex really potent, it would mean that any casual leakage of fluid from the bladder along the urethra, such as might occur with a sudden unexpected rise in intra-abdominal pressure, would, by abolishing the tonic contraction of the external sphincter of the urethra, lead to escape of urine, or at least make the voluntary maintenance of continence more difficult. Barrington (1915), in his very first paper on the nervous control of micturition, noted that, after putting the external urethral sphincter out of action by division of the pudendal nerves, the slightest pressure on the bladder through the abdominal wall caused escape of urine. On the other hand, Langworthy, Drew & Vest (1940) say that division of the pudendal nerve in cats caused no incontinence even when the cat was running or jumping. However this may be, when the bladder contracts the guarding reflex of the external urethral sphincter no longer operates. Instead, the external urethral sphincter relaxes, urine is forced along the urethra and this flow in turn maintains the contraction of the bladder. On this hypothesis the prime factor in inhibition of the tone of the external urethral sphincter in reflex micturition is the attainment of a critical tension in the bladder wall. We therefore suggest that there is no real evidence or argument for the existence of Barrington's fourth reflex in the cat: moreover, its existence might be a nuisance to such a cleanly animal.

The second and seventh reflexes in the cat—contraction of the bladder in response to perfusion of the urethra—can be elicited only at levels of bladder filling which are not far short of the critical point for the onset of micturition. These reflexes are not easy to demonstrate. Under normal circumstances, in the intact animal, these reflexes would obviously not be expected to initiate contraction of the bladder but only to maintain and reinforce a contraction already present. Denny-Brown & Robertson (1933) and Nathan (1952) could find no evidence for their existence in man. Our results in the cat, however, agree with those of Barrington. Similar effects have also been demonstrated by Langworthy, Kolb & Lewis (1940), so the cat does seem to have reflexes which are not present in man.

We are far from understanding the complexity of the reflexes which control micturition, still further from understanding the factors determining the nice relationship between urinary continence and micturition. So far as we can see at the moment, from Barrington's original work, from the series of papers by Langworthy and his colleagues, and from the present observations, the sequence is as follows.

As the bladder fills the muscular bladder wall adapts itself to the increasing volume with little increase in intravesical pressure. The tension in the wall, however, rises steadily as the radii of curvature increase. As filling continues, continence is assured by increased activity in the external urethral sphincter. Should urine enter the urethra at this stage the activity of the external sphincter is still further increased (the guarding reflexes).

When a critical tension develops in the bladder wall the micturition reflexes proper come into action. These probably operate in two stages:

Stage 1. Stimulation of the stretch receptors in series with the contractile elements in the bladder wall inhibits, through a 'centre' in the sacral cord, the existing tonic contraction in the striped muscle of the external urethral sphincter. The ingoing path is in the pelvic nerves, the outgoing in the pudendal nerves. This is Barrington's fifth reflex and it may come into play even before the following reflex.

Stimulation, presumably of the same receptors in series with the contractile elements in the bladder wall, initiates, through a 'centre' in the hind-brain, contraction of the detrusor muscle of the bladder. Both ingoing and outgoing paths are in the pelvic nerves. This is Barrington's first reflex.

About the same time stimulation, again acting somewhere in the bladder, causes reflex relaxation of the plain muscle in the wall of the proximal third of the urethra, the 'internal urethral sphincter'. The paths are again both in the pelvic nerves, but the 'centre' is in the sacral cord. This is Barrington's sixth reflex.

Stage 2. Since Barrington's fifth reflex is now in action, the flow of urine along the urethra no longer elicits the guarding reflex in the external sphincter. Instead, the flow of urine along the urethra maintains and perhaps reinforces the contraction of the bladder to ensure complete evacuation. Two reflexes play a part, Barrington's seventh reflex with both paths in the pelvic nerves and a 'centre' in the sacral cord, and his second reflex where the ingoing path is in the pudendal nerves, the 'centre' in the hind-brain, and the outgoing path in the pelvic nerves.

These reflexes presumably continue in action while the bladder is expelling its contents. Then, although the muscles in the bladder wall are still active, as the volume is reduced the area of the wall will also diminish. There will then come a point when the contractile elements have shortened as much as they can. A further reduction in wall area now relieves the tension on the receptors in series with the contractile elements and removes the stimulus from these receptors. The reflex drive is thus cut off and both the activation of the bladder wall and the inhibition of the external urethral sphincter subside.

If the receptors in the urethra are still active at this stage, they will produce reflex activity in the external sphincter now that the inhibition has been removed. This stops the escape of urine and the bladder then gradually refills from the ureters.

The above description ascribes (in the cat at least) no important role in micturition to Barrington's third reflex. The slight transitory rise of pressure in the bladder on distension of the urethra may be due, as Elliott (1907) claimed long ago, to contraction of a thin sheet of muscle spreading out from the ureters and trigone, muscle receiving a motor innervation from the sympathetic division of the autonomic nervous system. The existence of Barrington's fourth reflex, as an entity independent of the fifth reflex and of the other events during micturition, is denied for the reasons given in the body of this paper.

SUMMARY

1. The electrical activity of the striated external sphincter of the urethra was recorded while the pressure and volume of fluid within the bladder were varied: the effect on the external sphincter of forcing fluid along the urethra was also recorded.

2. In resting conditions the external sphincter showed a steady tonic discharge.

3. As the bladder filled there was initially an increase in the activity of the external sphincter. Ultimately the rise in tension in the wall of the bladder led to reflex contraction of the bladder and to cessation of activity in the external sphincter of the urethra; this cessation of activity was brought about both by active contraction of the bladder and by passive stretching of the wall of the bladder.

4. After spinal transection at the lower thoracic level, distension of the bladder no longer evoked reflex contraction of the bladder but did lead to cessation of activity in the external urethral sphincter.

5. When the bladder was empty, or deafferented by section of the pelvic nerves, forcing fluid distally along the urethra always augmented activity in the external urethral sphincter.

6. When the wall of the bladder was stretched passively, and when the bladder was contracting, forcing fluid distally along the urethra no longer evoked activity in the external sphincter.

7. No evidence was found to justify belief in the existence of Barrington's fourth reflex. This reflex implies that forcing fluid distally along the urethra by itself causes cessation of activity in the external urethral sphincter.

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